Evaluating the effectiveness of wildlife passages for small and medium sized mammals

April Robin Martinig

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Signed by the final examining committee:

Dylan Fraser Chair

Jochen Jaeger Supervisor

André Desrochers Supervisor

Jean-Philippe Lessard Examiner

James Grant Examiner

Grant Brown External Examiner

Approved by Patrick Gulick
Chair of Department or Graduate Program Director

November 2015 André G. Roy
Dean of Faculty

ABSTRACT

While many studies have looked at how large mammals respond to road mitigation measures, few have examined the effects on smaller mammals nor taken a multispecies approach. I investigated the effectiveness of three different types of wildlife passages along Highway 175 in Quebec for small and medium sized mammals (<30 kg) using infrared cameras. Wildlife passages (n=17) were monitored year round from 2012 to 2015. Two research questions were addressed: (1) Does discovery and use differ between passages and if so, why? and (2) Are there differences between species? Global and species-specific models were produced for both discovery and use. A linear mixed-effects model was used for discoveries (log-transformed counts) and a generalized linear mixed model was used for usage (binary response). Species' responded to the passages differently, with discoveries increasing overall and in particular for marmots (*Marmota monax*) as latitude increased. Pipe culverts were more likely to be discovered by micromammals and wooden ledge culverts by red squirrels (*Tamiasciurus hudsonicus*) than other passage types. Older passages were discovered less in general, with the exception of marmots. Marmots were the only species to show a difference in use by passage type, favouring pipe culverts. Passage use was less likely with a median present for all models, except squirrels. More open passages had higher use overall and particularly for marmots and weasels (*Mustela sp*). In contrast to previous studies, distance to cover and the presence of light were not important predictors. Agencies can engineer increasingly effective wildlife passages by minimizing the barrier effect of the structures themselves and constructing passages better suited to the needs of the species being targeted. To benefit the most species, it is recommended that future projects contain a diversity of open, single segment passages requiring long-term monitoring.

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INTRODUCTION

Habitat fragmentation is recognized as a major threat to regional biodiversity (Forman et al. 2003). Road infrastructure not only reduces the quantity and quality of the remaining habitat, but also acts as a barrier to wildlife movement and increases road mortality (Forman et al. 2003; Fahrig & Rytwinski 2009; Glista et al. 2009). These effects can mean a reduction in access to resources, limited gene flow, and restricted dispersal for species that are unable to overcome the presence of roads (Forman et al. 2003). The division of historically continuous populations into subpopulations increases the risk of extirpation as it inhibits reestablishment by immigrants (Forman et al. 2003). In an attempt to offset these consequences, it is becoming increasingly common to include wildlife passages along with road development (Clevenger & Waltho 2000; Glista et al. 2009).

An abundant body of literature has examined road management and mitigation for large mammals because of collisions with motorists (Clevenger & Waltho 2000; O'Connell et al. 2006; Glista et al. 2009; Huijser et al. 2009). Fewer studies have focused on small and medium sized mammals (Clevenger et al. 2001; McDonald & St. Clair 2004; Bellis et al. 2013). Yet, smaller mammals are also affected by habitat fragmentation (McGregor et al. 2008; Fahrig & Rytwinski 2009; Brehme et al. 2013) and play vital roles in the ecosystem (red-backed voles: Cook & MacDonald 2001 and Vanderwel et al. 2010; red squirrels: Goheen & Swihart 2003; beavers: Rosell et al. 2005 and Nummi &Holopainen 2014).

Transportation agencies have only recently constructing structures specifically designed for small fauna (Bédard et al. 2012). However, the efficacy of these passages remains largely untested (Clevenger et al. 2001; McDonald & St. Clair 2004; Bellis et al. 2013). Usage is only one part of a three step process. Before a passage is used, an animal must be present and may then investigate the structure. To my knowledge, no study has looked at what influences the discovery (combined presence and investigation) of a passage along with usage. Here, I investigated passage discovery and assessed use after an animal has entered the structure.

The specific attributes of interest are summarized in Table 1. Previous work has shown that passage success and species usage can be attributed to the structural and environmental characteristics of the passages (Clevenger & Waltho 2000, 2005; Clevenger et al. 2001). I hypothesize that passage type, openness, distance to cover, artificial light, year of construction, and the presence of a median influence passageway effectiveness. Apart from openness and passage type, which may vary among species, the other variables should have a similar effect across species (Clevenger & Waltho 2000, 2005; Clevenger et al. 2001). Open areas increase predation risk for small mammals, hence limited cover should decrease passageway discovery and use as body mass decreases (Clevenger et al. 2001; McDonald & St. Clair 2004; Clevenger & Waltho 2005). Areas of increased human activity are also generally avoided by wildlife, thus disturbance should be associated with reduced discovery (Rodriguez et al. 1996; Clevenger & Waltho 2000). Habituation to wildlife passages is also known to occur in larger mammals, suggesting older passages should be more frequently visited than those just recently constructed (Gagnon et al. 2011; Sawaya et al. 2013). Finally, an open median, although not yet investigated, should decrease the likelihood of a successful passage because it may act as an additional barrier to movement (McLaren et al. 2011; Clevenger & Kociolek 2013).

My study aims to answer two research questions: (1) Do the location and structure of passages explain differences in their discovery and use? and (2) Do the frequency of passageway discovery and use differ by species? To answer these questions, I investigated the effectiveness of targeted wildlife passages in Quebec for small and medium sized mammals using infrared cameras. My objective was to model how these species respond to wildlife passages, thereby providing targeted management recommendations for future development projects that intend to incorporate small fauna passages into the infrastructure design process.

METHODS

Study Site

Highway 175 lies in the Laurentian Mountains of the Laurentides Wildlife Reserve, a stretch of boreal forest connecting Quebec City and Saguenay. The vegetation in the Reserve can be characterized as homogenous, however it is mainly deciduous forest in the south and coniferous forest in the north. Community composition is consistent over the Reserve with a diversity of small and medium sized mammals present. In addition to those sampled in Table 2, Canadian lynx (*Lynx canadensis*), fishers (*Martes pennanti*), and gray wolves (*Canis lupus*) are known to be present. The species observed can be characterized as mainly nocturnal, territorial, and solitary species (see Appendix for complete life history traits for all sampled species).

From 2006 to 2012, safety issues resulted in expanding the highway from a two lane undivided road (spanning ~30 meters) to a four lane divided highway (spanning 90-150 meters) over 174 km (Bédard et al. 2012). Over the study period, average daily traffic volume ranged from 4,500 to 7,500 vehicles, with the highest levels in summer.

To help mitigate the effects of the expansion, the project included wildlife passages and exclusion fencing (Bédard et al. 2012). Along with six large fauna corridors, wildlife passages specifically targeting mammals smaller than wolves (<30 kg) were constructed between km 60 and 144 (Bédard et al. 2012). By 2012, only 19 of the planned 33 small fauna passages were retrofitted from existing transportation infrastructures, 17 of which were monitored year round from May 2012 to August 2015 along a 65 km portion of the highway (Figure 1) (Bédard et al.

2012). The underground culverts were grouped into three classes (Figure 2; Table 1). Mean distance between monitored passages was 3.82 km, but two passages were 323 m apart meaning a single individual could have visited both in a day. Culverts were assumed to be independent of each other for the purposes of statistical analysis. Passage elevation varied from 476 m to 820 m.

Data Collection

Infrared cameras (Reconyx™ HC600 Hyperfire H.D. Covert IR) were used in the passages because they allowed for continuous monitoring with minimal maintenance. Constant surveillance of all passages was not possible because cameras were occasionally lost due to theft or during spring thaw. Replacements were installed as soon as possible to minimize sampling differences. Camera sensors operated continuously, but only took photographs when motion-activated. They recorded five pictures/trigger and were installed facing in at all openings on the wall when a ledge was present (45 cm above the ledge) or on the ceiling when there was none. A reference block was placed in frame to estimate animal size. Cameras were visited once every two weeks from May to September to replace Secure Digital cards and nickel metal hydride batteries (≥15% charge). From October to April, lithium batteries were installed and cameras were visited periodically to check battery life. For a extensive description of the protocol consult Bélanger-Smith (2015).

Photos were stored in an ACCESS database where the location, date, temperature, time, direction of travel, species, age, sex, number of individuals, passage outcome, and behaviour were noted. Species that were difficult to distinguish were grouped at the level of genus or larger taxonomic group (weasels (*Mustela sp*) and micromammals (shrews, mice, voles, and moles)) (Table 2). Only the single best photo in the series was entered into the database and individuals were considered to be identical if they occurred within ten minutes of each other. When in doubt, fewer rather than more entries were made to avoid pseudoreplication. Unidentified animals were discarded from the analysis (2.6% of the observations).

Data Analysis

The independent variables were tested for multicollinearity and using a threshold lower than previous studies I removed highly correlated variables (Pearson's r>0.70) from the analysis (Table 1) (Clevenger et al. 2001 used r>0.75). Outliers were not removed because they were the result of legitimate sampling. An attempt was made to account for the confounding effects of spatial variation in species abundance on passage use, but the method employed (as seen in Rytwinski & Fahrig 2011) proved unreliable (see Discussion for a detailed explanation).

Global and species-specific models were produced for passage discovery and use. The majority of species were not observed frequently enough for reliable statistical inference. Only taxa with ≥100 observations were included in the models (Table 2). Micromammals (taxon) were only included in the species-specific models because their inclusion in the global models would overwhelm parameter estimation (Table 2). Functional traits (use of open areas or association with water) were used as fixed factors in the global models instead of species to allow for broader inference. Chipmunks (*Tamias striatus*), squirrels (*Tamiasciurus hudsonicus*), hares (*Lepus americanus*), and weasels were characterized as species that avoided open areas and water, marmots (*Marmota monax*) and porcupines (*Erethizon dorsatum*) as species that used open areas but avoided water, mink (*Neovison vison*) and muskrats (*Ondatra zibethicus*) as species that avoided open areas but used water, and skunks (*Mephitis mephitis*) as being associated with open areas and water (Naughton 2012).

Model simplification and selection were not conducted as care was taken to generate models with the fewest biologically relevant variables given *a priori* hypotheses about the study system. Statistical analysis was run in R, version 3.1.3 (2015), using the packages "lme4" and "lsmeans" (for pairwise comparisons) (Bates et al. 2015; Lenth 2015).

Modelling Passageway Discovery

A linear mixed-effects model was used because the count data, once log-transformed, met the assumption of Gaussian distributed residuals and still allowed for fixed and random effects. Each instance of an individual arriving at a passage entrance was considered a single, independent event.

The global discovery model included year of construction, distance to cover, artificial light, location, type, and species-specific functional traits as fixed factors and species and culvert identity as random effects. Species-specific discovery models included year, distance to cover, artificial light, type, and location as fixed factors and culvert identity as a random effect. Log transforming distance to cover did not change model output.

R code for models:

- discovery <- lmer (log(count + 0.1) ~ type + year + distance + light + km + open + water + (1|species) + (1|culvertID), data = x)
- species <- lmer (log(count + 0.1) ~ type + year + distance + light + km + (1|culvertID), data = x))

Modelling Passageway Use

A generalized linear mixed model was best suited for the data because it allowed for a binomial response variable with fixed and random effects. The binomial response was crossing, rated as a non-crossing when only seen in one segment (partial crossing), one camera (unknown crossing), or entering and exiting on the same camera (exploration). To be rated as a complete crossing, an individual of the same species had to be seen in at least two cameras, traveling in the same direction, and within ten minutes of the first photo as crossings rarely took longer than this. Limiting the number of observations a single individual contributed to the analysis minimized pseudoreplication, but did not help differentiate among individuals (Hurlbert 1984). This is a limitation of camera data (Ford et al. 2009).

The global use model included type, distance to cover, openness, presence of a median, and species-specific functional traits as fixed factors and species and culvert identity as random effects. Species-specific use models included type, distance to cover, openness, and presence of a median as fixed factors and culvert identity as a random effect. Log transforming distance to cover did not change model output.

R code for models:

- use <- glmer (passage ~ type + openness + median + distcov + open + aquatic + (1|species) + (1|culvertID), family = binomial (link = logit), data = x, control = glmerControl (tol = 1e-6, optimizer = "bobyqa", optCtrl = list(maxfun = 1e9)))
- species <- glmer (passage ~ type + openness + median + distcov + (1|culvertID), family = binomial(link = logit), data = subset(x, species == "species"), control = glmerControl(tol = 1e-6, optimizer = "bobyqa", optCtrl = list(maxfun = 1e9)))

RESULTS

I analyzed 227,720 photos over the study period, 97,889 of which were of mammals (43%) and the remaining 57% were other species (birds, humans, frogs, etc.) or caused by the elements (rain, wind, snow, etc.). I documented 14,344 independent observations representing at least 18 faunal groups (Figure 3). Of these, 13% resulted in a complete passage, 59% were unknown, and 28% were exploratory. Micromammals accounted for 56% of sightings, followed by red squirrels (13%), marmots (10%), weasels (9.5%), and mink (4%). Pipe culverts (success rate: 12.6%±0.3) had the most discoveries and crossings, followed by wood (success rate: 13.3%±0.3) and concrete culverts (success rate: 12.9%±0.3). Marmots crossed the most overall (36%) and had the highest usage per visit (44%), followed by micromammals with an overall crossing rate of 20% but only 4.5% use per visit, weasels (15% overall crossing rate and 20% use), red squirrels (11% overall crossing and use rates), and mink (10% overall crossing rate and 34% use) (Figure 3 and 4).

Passageway Discovery Results

Counts significantly decreased by year, while increasing for passages further north (Table 3). Counts were not significantly affected by passage type, distance to cover, the presence of artificial light, or species use of open areas or association with water (Table 3).

Counts significantly decreased by year for all species but marmots (Figure 6; Table 4). Passages further north had significantly higher counts for marmots and did not have a significant effect for micromammals, mink, weasels, and squirrels (Figure 6; Table 4). Distance to cover did not have a significant effect on counts for all species, nor did artificial light (Table 4). Passage type only had a significant effect on counts for micromammals (PCs were discovered more than both types of box culverts) and squirrels (DWCs were discovered more than DCCs) (Figure 7; Table 4).

Passageway Use Results

More open passages experienced significantly higher use, but when a median was present use significantly decreased (Table 5). Use was not significantly higher for species that used open areas or were associated with water, nor did it differ between passage types or distance to cover (Table 5).

Squirrels were the only species for which use was unrelated to the presence of a median (Table 6). All other species were less likely to cross when a median was present (Table 6). Passages with higher openness ratios experienced significantly more crossings for marmots and weasels (Table 6). Openness had no effect on use for micromammals, mink, and squirrels (Table 6). Marmots were the only species were passage type affected use, crossing pipe culverts more than box culverts (Table 6). Distance to cover had no effect on use for all species (Table 6).

Discussion

Crossing success of smaller mammals was associated with the location and structural characteristics of the monitored passages. Overwhelmingly, discovery decreased over time. This may be a reflection of regional trends in abundances or possibly a decline in investigations. A previous study which found that vole fluctuations followed a four year cycle in Quebec offers one explanation for the negative trend observed across species (Cheveau et al. 2004). A spike in observations corresponded to when micromammals were supposed to be at a population peak in 2012 and this trend may hold loosely across species (Figure 8) (Yanes et al. 1995; Cheveau et al. 2004). Alternatively, it is possible that investigations of the passages declined regardless of abundances if the novelty of the structures decreased over time. Although individuals may be present in the landscape, their inclination to investigate the structure may be diminished if they previously explored it at an earlier time. It is conceivable that monitoring may have ceased too quickly to assess any real effect of the passages. Thus, post-mitigation studies should be longer than seen here.

Paradoxically, one common theme was that passage type ranked low as a factor that affected not only passage discovery, but use. Pipe culverts were discovered more by micromammals and wooden ledge box culverts more by red squirrels. Both species were distributed over the whole study area, however only micromammals discovered all passages. For squirrels, three passages accounted for 87% of the visits and the remainder experienced 0 to 50. Discoveries were not distributed over the whole area, but rather clustered in the southern portion of the site. It is possible that squirrels prefer wooden ledges, however their lack of discoveries at all passages north of KM 89 (despite there being DWC passages present) is suggestive that passage type is not the only factor at play.

An environmental gradient could also exaggerate differences in passage discovery. If a gradient in landscape features produced environmental conditions that significantly changed along the highway this would affect community composition (Clevenger & Waltho 2005; Mata et al. 2005). Contrary to the clustering seen in red squirrels, the latitudinal increase in discoveries overall and, in particular, for marmots may be confounded by their distribution over the environment. Only four passages were discovered by large numbers of marmots (>50) and just one is located in the south. This may reflect a discontinuity in the population as the habitat between the south and north is heavily forested with little verge along the highway. Marmots rely on open areas to survive and they may not be present in the environment at certain points along the highway which could explain the latitudinal gradient (Naughton 2012).

Crossings were also higher for more open passages. Venturing into the open can expose smaller mammals to predation, however animals that regularly use open areas may be more comfortable in this environment allowing them to explore and successfully use the passages (Clevenger et al. 2001; McDonald & St. Clair 2004). The ability to effectively employ predator avoidance mechanisms require the potential to survey the environment (McDonald & St. Clair 2004; Clevenger & Waltho 2005). This may be why passages that allow for increased visibility are favoured overall and particularly by marmots and weasels. When smaller mammals resist crossing passages with low openness ratios this could be reinforcing the barrier effect in longer, less open passages (Mader 1984; Ascensão & Mira 2007).

Segmented passages, on the other hand, have the advantage of a higher openness ratio, however this comes at the cost of interrupting movement across the highway. The presence of a median appears to pose a disadvantage as use decreased across all models, but did not affect squirrels. These results highlight the need to limit additional barriers to wildlife movement across highways, something that should be considered in the planning stages of development (Ascensão & Mira 2007). Additionally, the habitat provided by the median may be of interest as it is possible that individuals were using the passages to forage, rather than to cross (McLaren et al. 2011).

When Science Meets Reality

There are several possible sources of noise in the data. First, by focusing my efforts on multiple species, I achieved a higher scale of resolution but this assumed equal detection across species. Camera data are biased towards wildlife that are slow moving, large, and have higher rates of dispersal (O'Connell et al. 2006; Ford et al. 2009; Popescu et al. 2014). Focusing on small and medium sized mammals did not eliminate this.

Second, given the scale of the study, it was not possible to account for variation in the density of drainage culverts and wildlife passages in the study area. Culvert isolation may be a confounding variable, thereby affecting the ecological significance of my conclusions (Clevenger & Waltho 2005; Ascensão and Mira 2007). For example, high passage use may be due to there being no other suitable passages nearby rather than because there is active selection occurring.

Another well established source of variation that I could not reliably access were differences in wildlife abundances near the passages. This was the result of uncontrolled physical, biological, and anthropogenic factors (topography, seasonality, habituation threshold, home range size, sampling methods, experimental design, technician error, track identification uncertainty, data unreliability, etc.) (MacKenzie et al. 2002; McDonald and St. Clair 2004; O'Connell et al. 2006; Stephens et al. 2006; Larrucea et al. 2007; Treves et al. 2010; Sollmann et al. 2013). It is recognized that the explanatory power of the models are diminished without accounting for this confounding variable, however the costs of inclusion would outweigh the benefits (Hardy et al. 2003; MacKenzie 2005; Bailey et al. 2007; van der Grift et al. 2013).

Implications for Managers

Despite these cautions, my study has important management implications. Mitigation planning has progressed past the stage of simply evaluating passageway use, leaving more to be desired from the methods employed. Infrared cameras only provide information on the use of structures by wildlife. Future mitigation studies should not be restricted to this approach when analyzing passageway effectiveness. Most attempts to go beyond this level of analysis are labour intensive and costly, but a simple solution may exist through using subcutaneous radio tags (van Vuurde & van der Grift 2005; Baxter-Gilbert et al. 2015). Individual use of the passages could be estimated without further complicating the analysis.

This also brings up the question of how much passage use is enough. Transportation agencies are urged to take a proactive approach to wildlife mitigation with pre- and post-development research if more robust answers are desired about the effectiveness of the measures they have chosen to employ (Corlatti et al. 2009; Bellis et al. 2013). Without clear objectives, studies such as this one are only able to provide general guidelines.

Lastly, more collaboration is needed at all levels of planning, particularly concerning passage placement (van der Grift et al. 2013). Placing passages where wildlife actually cross the roads should, in theory, increase efficacy (Eberhardt et al. 2013). Studies that look at wildlife mortality along highways can identify such hotspots (van Vuurde & van der Grift 2005; Bissonette & Adair 2008; Ford et al. 2011).

Conclusion

This study highlights ways in which agencies can engineer increasingly effective small fauna passages through minimizing the barrier effect of the structures themselves by constructing more open, unsegmented passages. By looking at passage use and discovery simultaneously, I have shown it is possible to evaluate not only passage use, but what may influence an animal's decision to investigate the structure initially. The results obtained here are site and community specific, so it is important to emphasize that having a diversity of wildlife passages would likely be best suited to serve the widest range of animals given the life-history variation between and within taxonomic groups (Clevenger et al. 2001; McDonald & St. Clair 2004; Clevenger & Waltho 2005; Baxter-Gilbert et al. 2015). As transportation agencies plan future infrastructure development projects there remains one take home message for them to consider: *variety is the spice of life*.

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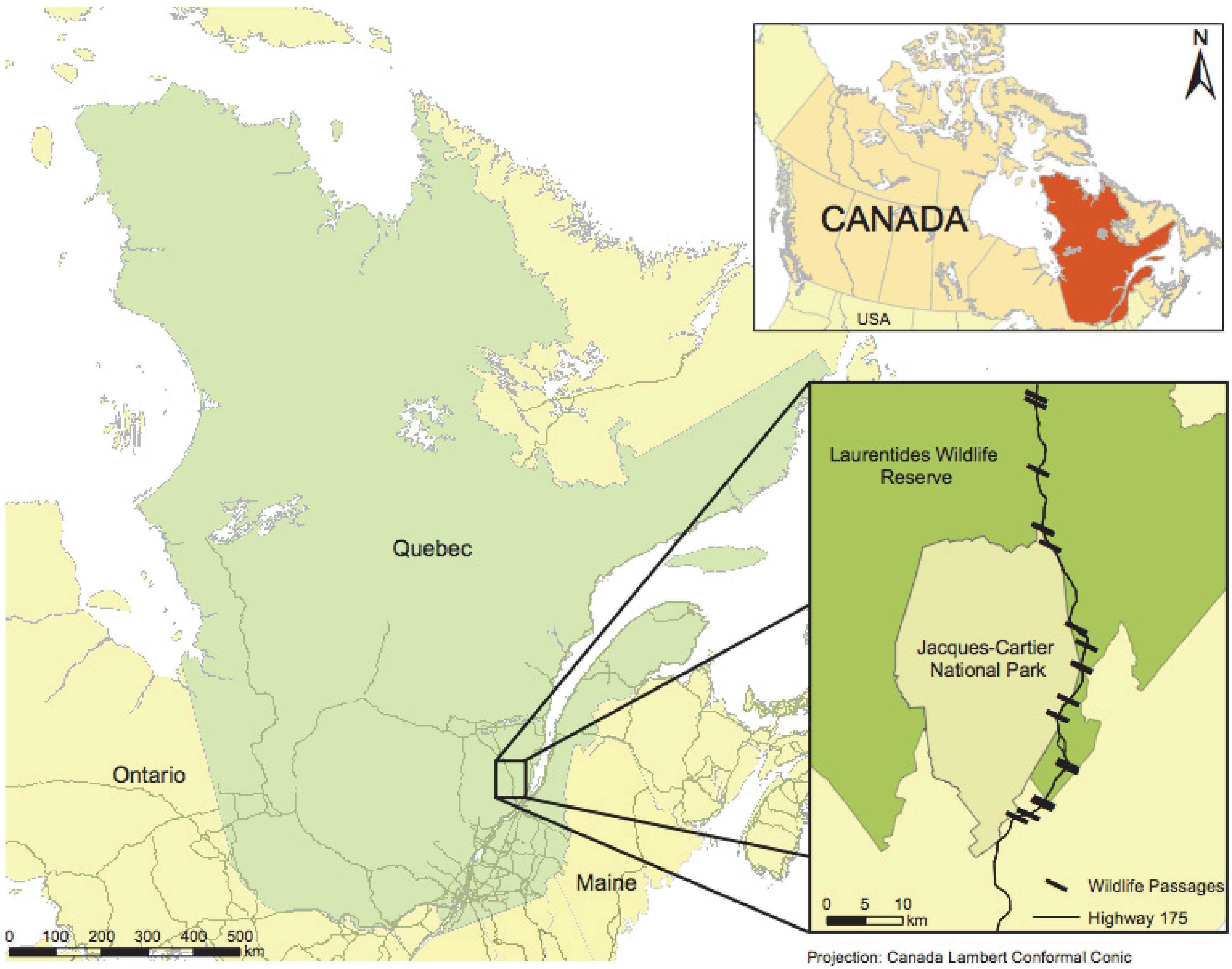

Figure 1. Study area and locations for the passages monitored (n=17) from 2012 to 2015 along Highway 175, Quebec, Canada.

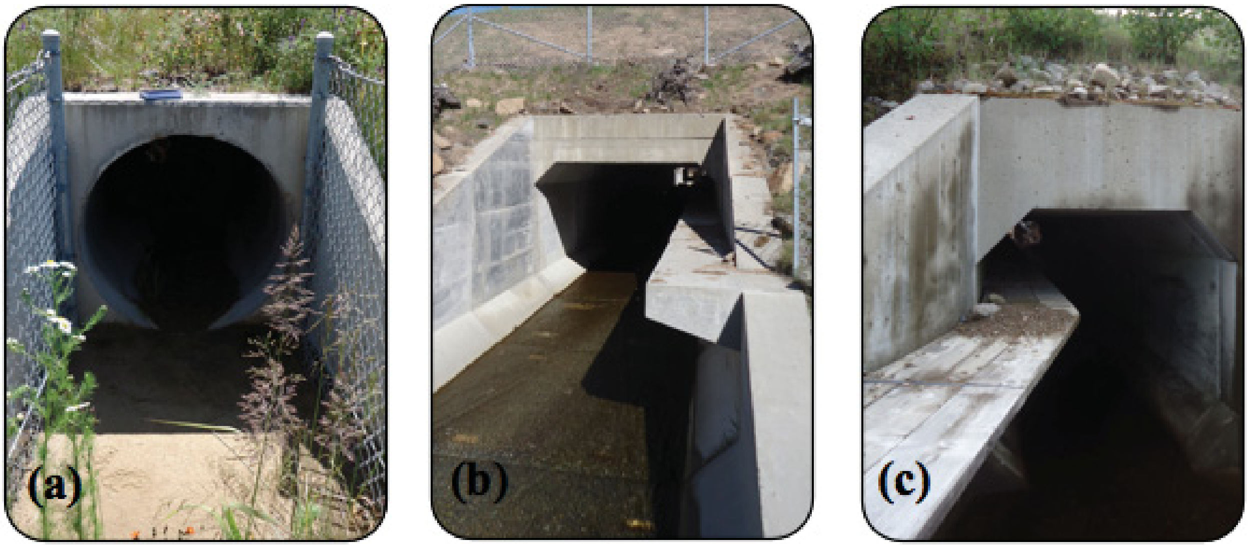

Figure 2. The different wildlife passage types monitored with infrared cameras from 2012 to 2015 along Highway 175, Quebec, Canada. (a) Pipe culvert (PC) (n=6). (b) Box culvert with dry concrete ledge (DCC) (n=7). (c) Box culvert with dry wooden ledge (DWC) (n=4). Pictures are not to scale.

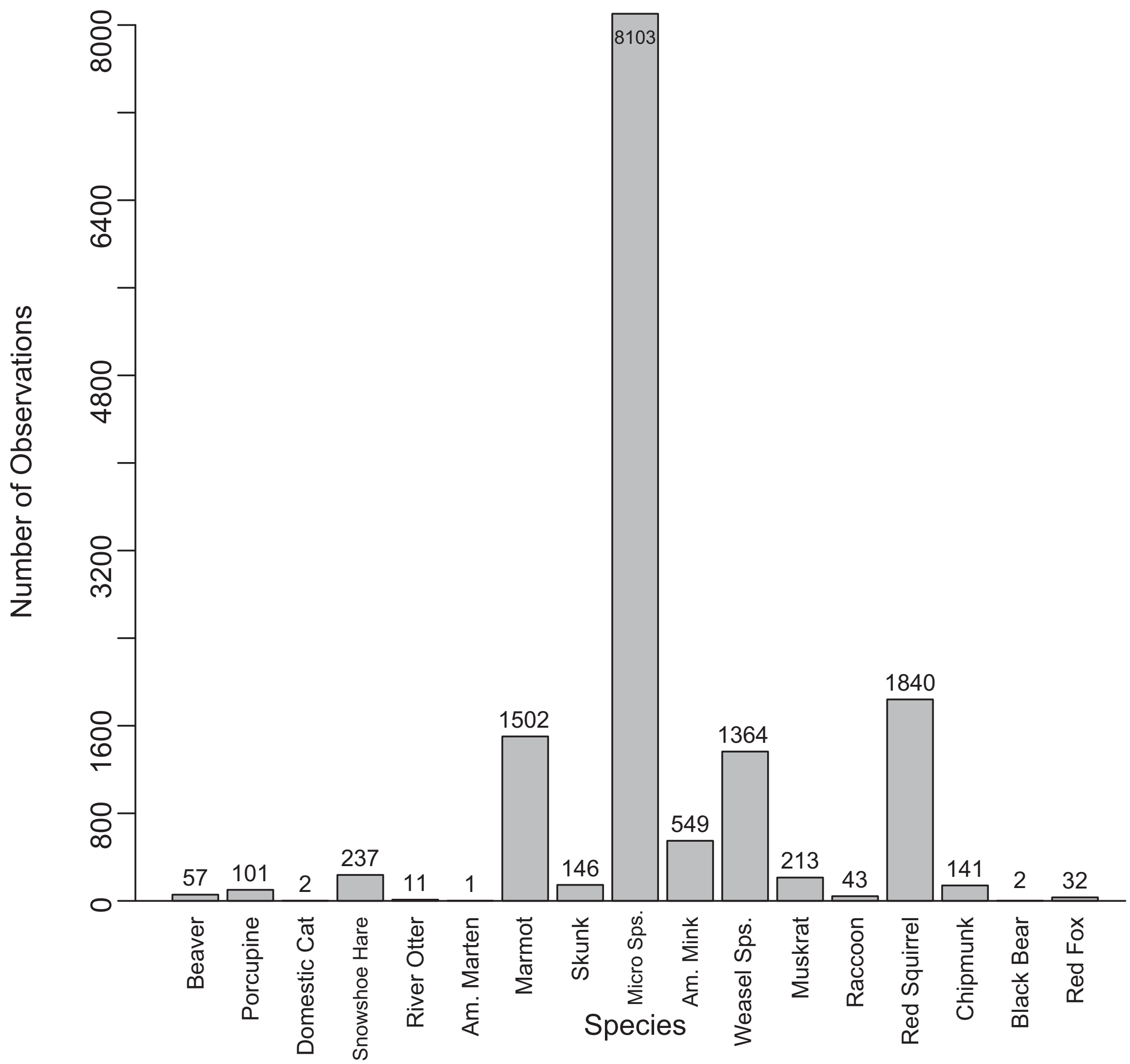

Figure 3. Number of mammal observations at 17 wildlife passages along Highway 175, Quebec, Canada, based on camera stations from 2012 to 2015. Numbers above bars are totals. See Table 2 for scientific names of species.

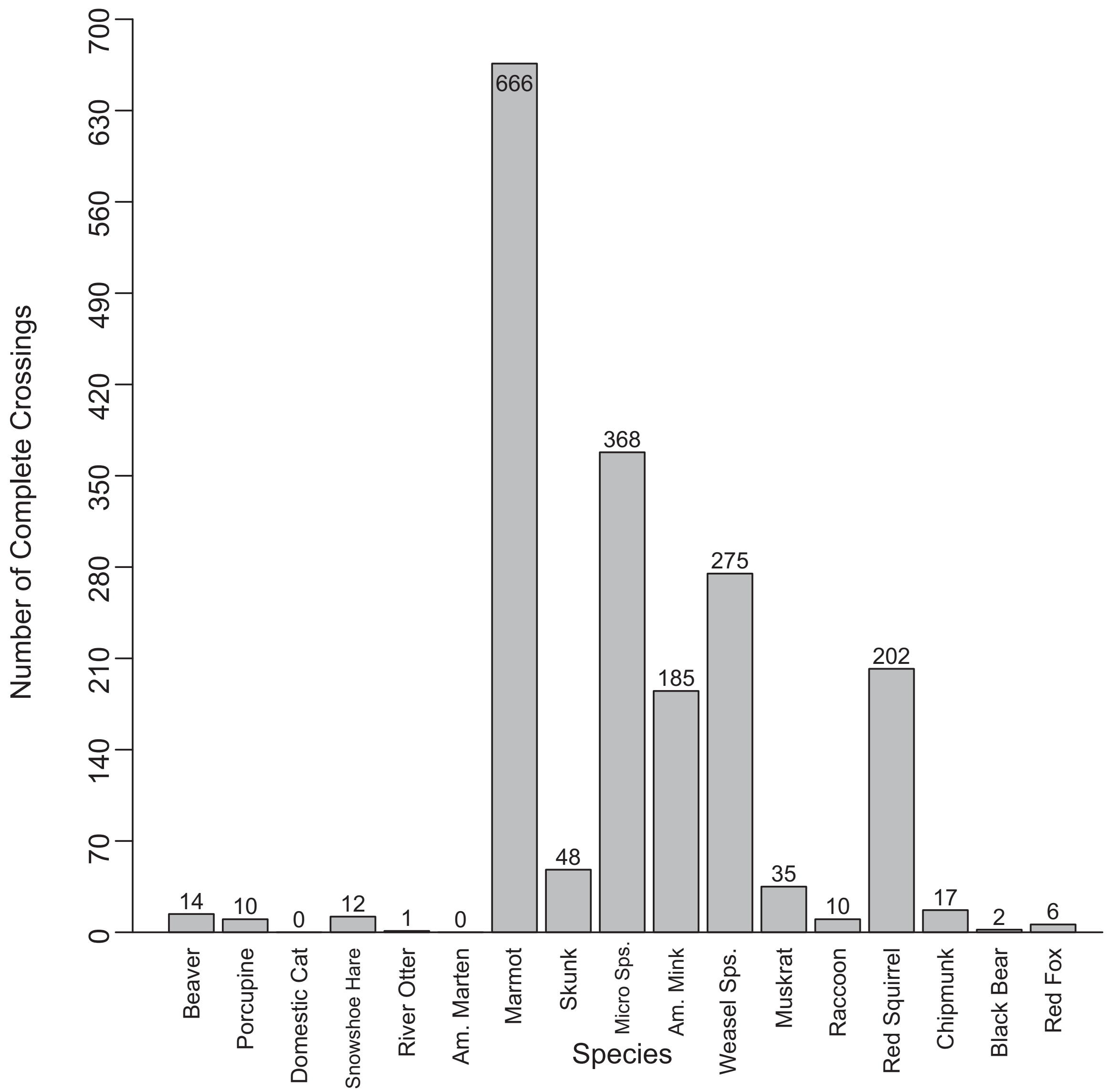

Figure 4. Number of mammal crossings at 17 wildlife passages along Highway 175, Quebec, Canada, based on camera stations from 2012 to 2015. Numbers above bars are column totals. See Table 2 for scientific names of species.

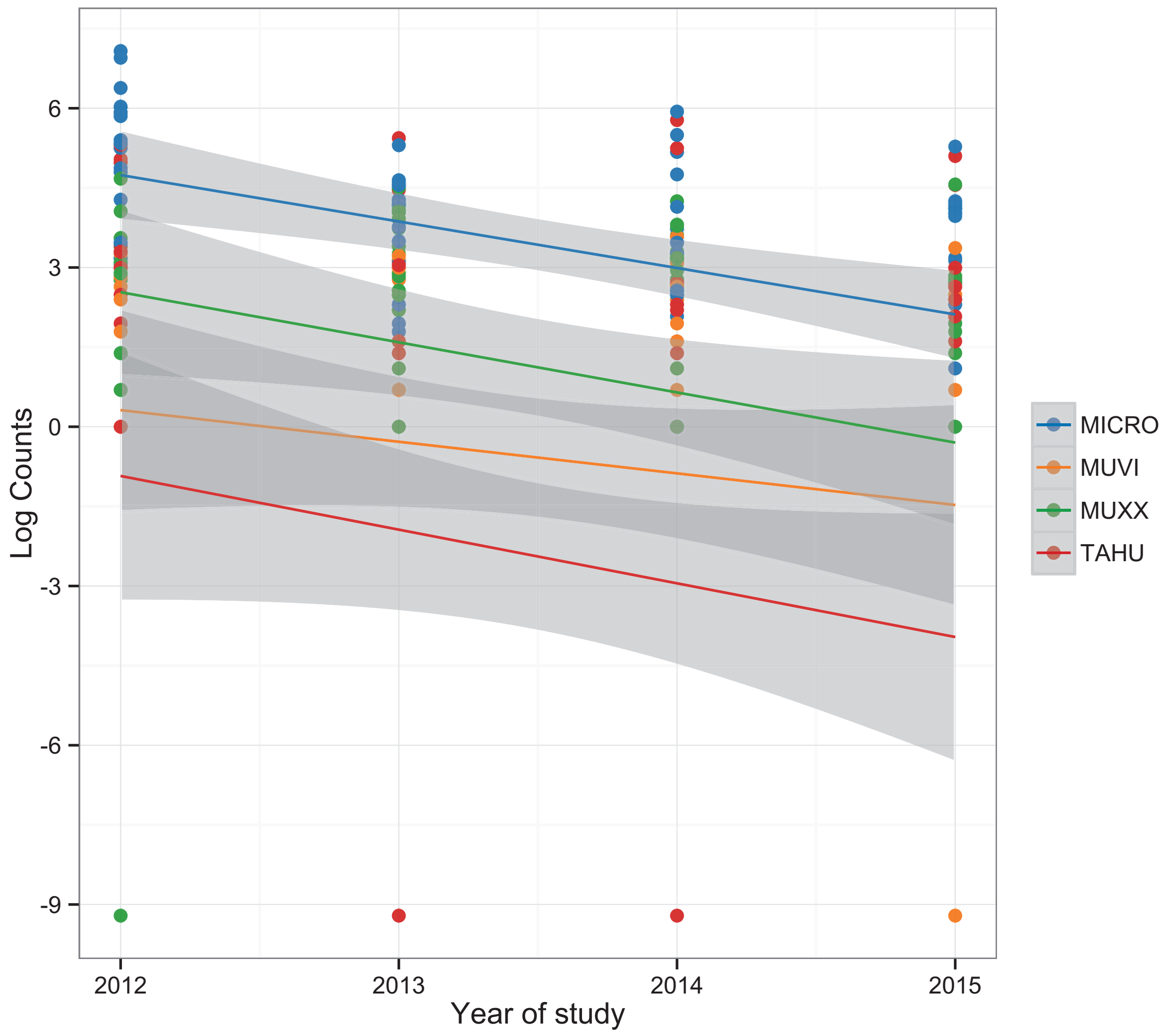

Figure 5. Relationship between year of study and number of sightings (log transformed) for micromammals (MICRO, n=7776), American mink (MUVI, n=494), weasels (MUXX, n=1247), and red squirrels (TAHU, n=1711). Shading around maximum likelihood lines represents standard error.

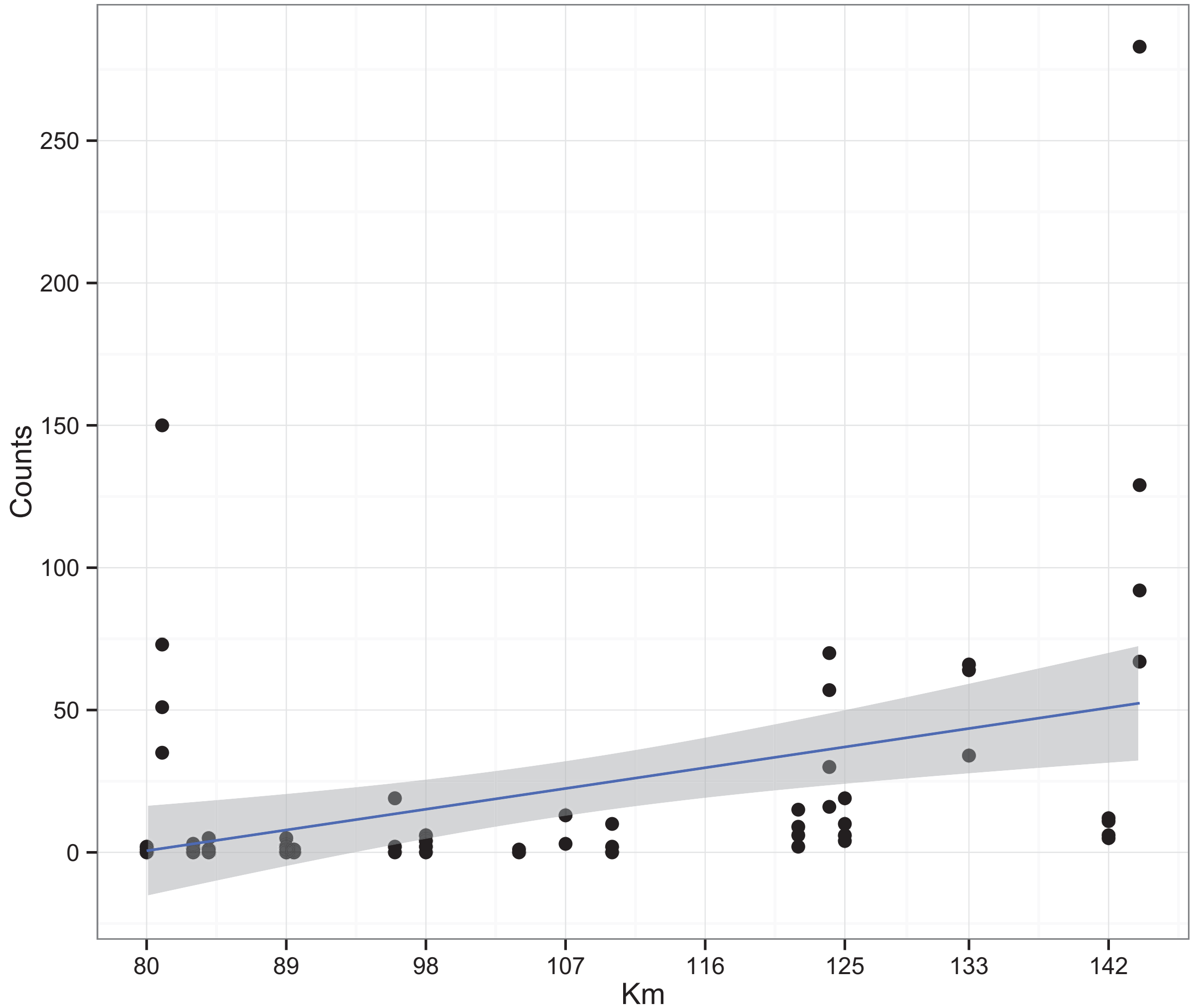

Figure 6. Relationship between location (km) and number of sightings of marmots (n=1349).

Shading around maximum likelihood lines represents standard error.

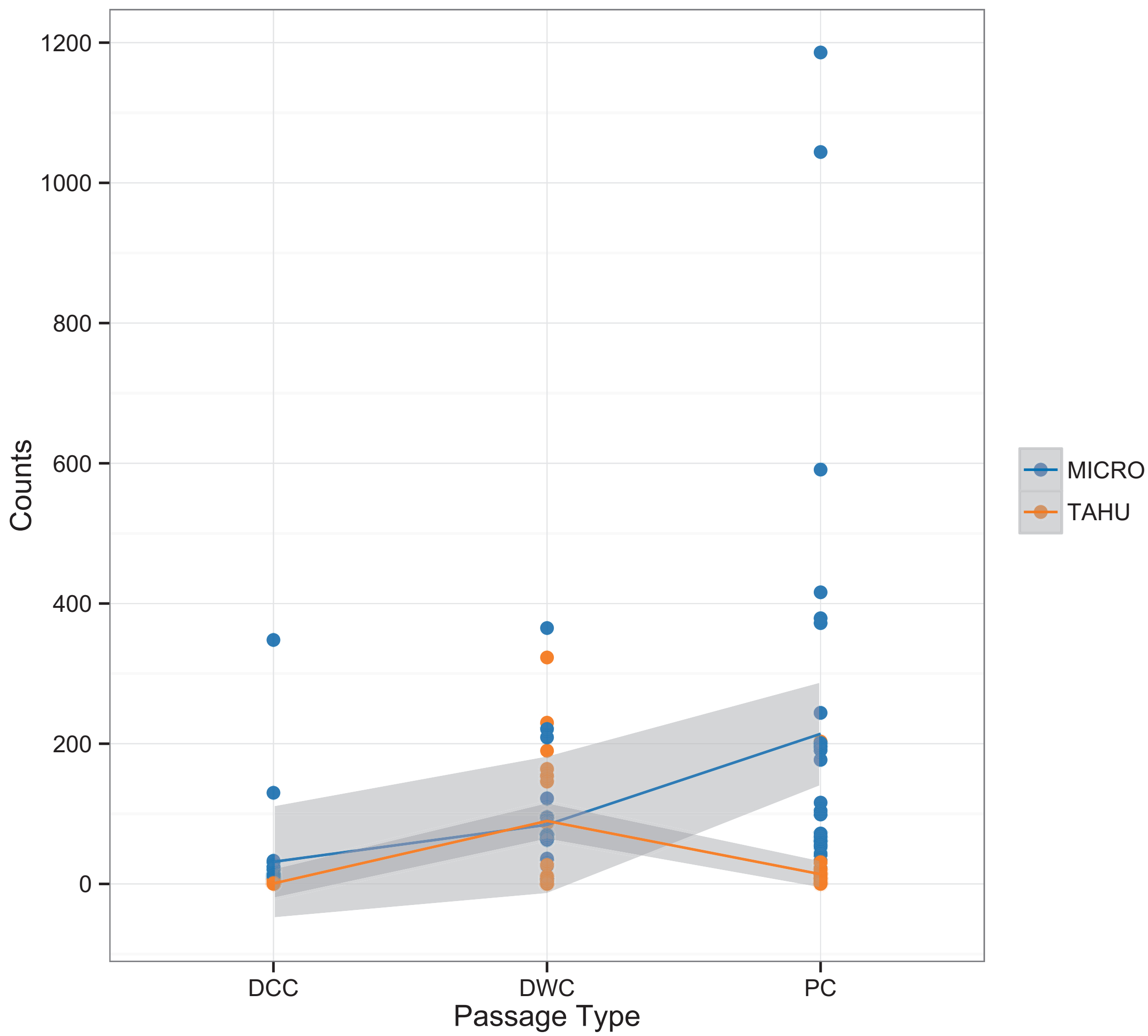

Figure 7. Relationship between passage type and number of sightings for micromammals (n=8103) and red squirrels (n=1840). Shading around maximum likelihood lines represents standard error.

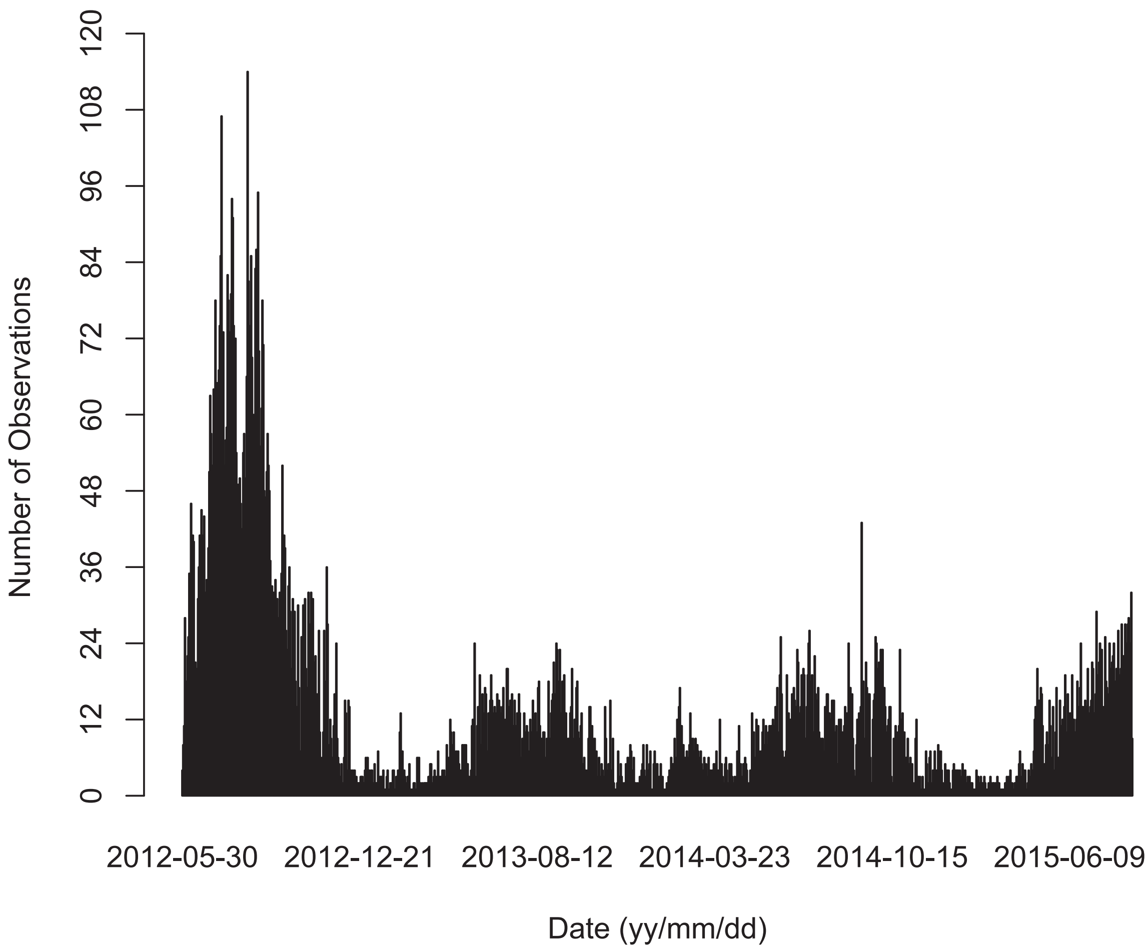

Figure 8. Number of observations per day from 2012 to 2015 for the wildlife passages (n=17) along Highway 175, Quebec, Canada.

Table 1. Names, definitions, and range for the 11 attributes considered in the analysis of the monitored wildlife passages (n=17) along Highway 175, Quebec, Canada (2012 to 2015).

Attribute	Definition	Range
PASSAGE STRUCTURE		
Passage type[a]	Pipe culvert (PC) Box culvert with dry concrete ledge (DCC) Box culvert with dry wooden ledge (DWC)	n=6 n=7 n=4
Openness	Culvert width x culvert height/culvert length[b] (m)	0.004-0.50
HABITAT & ROAD		
Median	Presence, Yes (1) / No (0)	0-1
Distance to cover	Average distance (m) to nearest continuous forest from passage entrance	6-105
Wildlife fence[cd]	0=small[e] fauna fence, 1=large[f] and small[e] fauna fence	0-1
Road lighting	Presence, Yes (1) / No (0)	0-1
Location	Location of passage (km)	80-144
Year of construction	When study was constructed (year)	2007-2012
SPECIES FUNCTIONAL TRAITS[g]		
Body mass[ch]	Log_{10} of average body mass (g)	1.98-3.78
Open areas	Use (1) or avoidance (0) of open areas	0-1
Water obligate	Association with (1) or avoidance of (0) water	0-1

[a] See Figure 2 for photos of each passage type
[b] Reed & Ward 1985
[c] Removed from analysis due to multicollinearity (Pearson's r>0.70)
[d] Correlated with *Location*
[e] Small mesh (1 inch x 1 inch), 2.5 feet tall
[f] Large mesh (5 inch x 12 inch), 12 feet tall
[g] Naughton 2012
[h] Correlated with *Open Areas*

Table 2. Species observed (common name, scientific name, and species code) in the monitored wildlife passages (n=17) along Highway 175, Quebec, Canada (2012 to 2015).

Common Name	Scientific Name	Species Code
American beaver	*Castor canadensis*	CACA
Porcupine	*Erethizon dorsatum*	ERDO[a]
Snowshoe hare	*Lepus americanus*	LEAM[a]
River otter	*Lontra canadensis*	LOCA
American Marten	*Martes americana*	MAAM
Marmot/Groundhog	*Marmota monax*	MAMO[ab]
Striped skunk	*Mephitis mephitis*	MEME[a]
White-footed mouse Jumping mouse Vole and bog lemming Shrew Star-nosed Mole	*Peromyscus leucopus* *Zapus sp* Family*: Cricetidae* *Sorex sp* *Condylura cristata*	MICRO[b]
American mink	*Neovison vison*	MUVI[ab]
Ermine Long-tailed Weasel	*Mustela erminea* *Mustela frenata*	MUXX[ab]
Common muskrat	*Ondatra zibethicus*	ONZI[a]
Racoon	*Procyon lotor*	PRLO
Red squirrel	*Tamiasciurus hudsonicus*	TAHU[ab]
Eastern chipmunk	*Tamias striatus*	TAST[a]
Black bear	*Ursus americanus*	URAM
Unknown animal	-	UNKN
Red fox	*Vulpes vulpes*	VUVU

[a] In global models
[b] Has own species-specific model

Table 3. Parameter estimates from the linear mixed model (df=9) with number of passage discoveries as a response variable (n=6093).

Variable	Estimate	SE	*t*	χ^2	Confidence limits (95%)		*p*
Type Wooden (DWC)[a]	0.91	0.57	1.60	-	-0.067	1.90	0.25
Type Pipe (PC)[a]	1.03	0.48	2.14	-	0.020	1.85	0.083
Comparison PC - DWC[a]	0.11	0.60	0.19	-	-0.91	1.14	0.98
Year	-0.22	0.063	-3.49	12.2	-0.34	-0.096	<0.001*
Distance to Cover	-0.015	0.015	-0.96	0.92	-0.041	0.012	0.34
Presence of Light	-0.30	0.79	-0.37	0.14	-1.66	1.07	0.71
Km	0.027	0.010	2.67	7.11	0.0096	0.44	0.0077*
Use of Open Areas	0.084	0.97	0.086	0.007	-1.66	1.83	0.93
Associated with Water	-0.30	0.97	-0.31	0.098	-2.05	1.44	0.75

[a] Output obtained from pairwise comparison.

Table 4. Parameter estimates from the linear mixed model output (df=7) with number of passage discoveries as a response variable by marmots (n=1502), micromammals (n=8103), American mink (n=549), weasels (n=1364), and red squirrels (n=1840).

Variable	Estimate	SE	t	χ^2	Confidence limits (95%)		p
MARMOTS							
Type Wooden (DWC)[a]	1.74	1.05	1.66	-	-0.013	3.49	0.22
Type Pipe (PC)[a]	1.83	0.88	2.08	-	0.036	3.31	0.095
Comparison PC - DWC[a]	0.093	1.10	0.085	-	-1.74	1.92	0.996
Year	-0.12	0.15	-0.76	0.58	-0.42	0.19	0.45
Distance to Cover	0.037	0.028	1.31	1.72	-0.010	0.084	0.19
Presence of Light	-1.50	1.46	-1.03	1.06	-3.94	0.93	0.30
Km	0.063	0.019	3.394	11.5	0.032	0.094	<0.001*
MICROMAMMALS							
Type Wooden (DWC)[a]	0.82	0.65	1.25	-	-0.27	1.90	0.42
Type Pipe (PC)[a]	2.53	0.55	4.60	-	1.61	3.44	<0.001*
Comparison PC - DWC[a]	1.71	0.68	2.51	-	0.57	2.85	0.032*
Year	-0.747	0.12	-6.30	39.7	-0.98	-0.51	<0.001*
Distance to Cover	0.018	0.018	1.04	1.09	-0.011	0.048	0.30
Presence of Light	-0.29	0.91	-0.32	0.10	-1.80	1.23	0.75
Km	0.016	0.012	1.38	1.90	-0.0033	0.035	0.17
MINK							
Type Wooden (DWC)[a]	0.88	1.01	0.87	-	-0.81	2.57	0.66
Type Pipe (PC)[a]	-0.63	0.85	-0.75	-	-2.06	0.79	0.74
Comparison PC - DWC[a]	-1.51	1.06	-1.43	-	-3.28	0.25	0.32
Year	-0.31	0.15	-2.00	4.01	-0.61	-0.0039	0.045*

Variable	Estimate	SE	t	χ^2	Confidence limits (95%)		p
Distance to Cover	-0.040	0.027	-1.46	2.13	-0.085	0.0058	0.14
Presence of Light	-0.74	1.40	-0.53	0.28	-3.09	1.61	0.60
Km	0.019	0.018	1.05	1.09	-0.011	0.049	0.30
WEASELS							
Type Wooden (DWC)[a]	1.09	1.04	1.05	-	-0.64	2.82	0.54
Type Pipe (PC)[a]	1.92	0.87	2.21	-	0.047	3.37	0.070
Comparison PC - DWC[a]	0.83	1.08	0.77	-	-0.97	2.63	0.72
Year	-0.46	0.14	-3.37	11.4	-0.72	0.19	<0.001*
Distance to Cover	-0.014	0.028	-0.51	0.26	-0.060	0.032	0.61
Presence of Light	-0.50	1.44	-0.35	0.12	-2.90	1.90	0.73
Km	-0.0019	0.018	-0.104	0.011	-0.032	0.029	0.92
SQUIRRELS							
Type Wooden (DWC)[a]	4.45	1.47	3.02	-	1.99	6.90	0.0071*
Type Pipe (PC)[a]	2.19	1.24	1.77	-	-0.12	4.25	0.18
Comparison PC - DWC[a]	-2.26	1.53	-1.47	-	-4.82	0.30	0.30
Year	-0.37	0.14	-2.71	7.34	-0.64	-0.099	0.0067*
Distance to Cover	-0.019	0.039	-0.47	0.22	-0.085	0.047	0.64
Presence of Light	-0.33	2.04	-0.16	0.026	-3.74	3.08	0.87
Km	0.026	0.026	0.99	0.99	-0.018	0.069	0.32

[a] Output obtained from pairwise comparison.

Table 5. Parameter estimates from the generalized linear mixed model (df=8) with passage use as a response variable (n=6093).

Variable	Estimate	SE	*z*	Confidence limits (95%)		*p*
Type Wooden (DWC)[a]	-0.34	0.31	-1.09	-0.95	0.27	0.27
Type Pipe (PC)[a]	0.34	0.25	1.40	-0.14	0.83	0.16
Comparison PC - DWC[a]	0.69	0.25	1.98	0.0047	1.37	0.12
Openness	2.63	0.79	3.35	1.09	4.17	<0.001*
Presence of a Median	-1.08	0.25	-4.29	-1.57	-0.59	<0.001*
Distance to Cover	-0.0057	0.0069	-0.82	-0.019	0.0079	0.41
Use of Open Areas	0.62	0.53	1.18	-0.41	1.65	0.24
Associated with Water	0.47	0.52	0.90	-0.56	1.49	0.37

[a] Output obtained from pairwise comparison.

Table 6. Parameter estimates from the generalized linear mixed model (df=6) with passage use as a response variable by marmots (n=1502), micromammals (n=8103), American mink (n=549), weasels (n=1364), and red squirrels (n=1840).

Variable	Estimate	SE	z	Confidence limits (95%)		p
MARMOTS						
Type Wooden (DWC)[a]	0.11	0.32	0.34	-0.52	0.73	0.94
Type Pipe (PC)[a]	0.95	0.26	3.68	0.44	1.45	<0.001*
Comparison PC - DWC[a]	0.84	0.35	2.41	0.16	1.52	0.042*
Openness	1.76	0.28	6.31	1.22	2.31	<0.001*
Presence of a Median	-0.77	0.27	-2.83	-1.30	-0.24	0.0046*
Distance to Cover	0.0033	0.0056	0.58	-0.0078	0.014	0.56
MICROMAMMALS						
Type Wooden (DWC)[a]	0.73	0.71	1.02	-0.67	2.13	0.56
Type Pipe (PC)[a]	0.70	0.56	1.25	-0.40	1.81	0.42
Comparison PC - DWC[a]	-0.027	0.74	-0.036	-1.46	1.40	0.999
Openness	-1.01	1.75	-0.58	-4.43	2.41	0.56
Presence of a Median	-1.53	0.56	-2.75	-2.62	-0.44	0.0061*
Distance to Cover	0.0032	0.015	0.21	-0.026	0.032	0.83
AMERICAN MINK						
Type Wooden (DWC)[a]	0.055	0.50	0.11	-0.92	1.03	0.99
Type Pipe (PC)[a]	-0.41	0.44	-0.94	-1.28	0.45	0.62
Comparison PC - DWC[a]	-0.47	0.60	-0.79	-1.64	0.70	0.71

Variable	Estimate	SE	z	Confidence limits (95%)		p
Openness	-1.11	2.05	-0.54	-5.12	2.90	0.59
Presence of a Median	-1.09	0.49	-2.24	-2.05	-0.14	0.025*
Distance to Cover	-0.0013	0.011	-0.12	-0.023	0.021	0.91
WEASELS						
Type Wooden (DWC)[a]	-0.58	0.35	-1.68	-1.26	0.096	0.21
Type Pipe (PC)[a]	-0.21	0.26	-0.83	-0.71	0.29	0.69
Comparison PC - DWC[a]	0.37	0.38	0.98	-0.37	1.12	0.59
Openness	3.14	0.81	3.85	1.54	4.74	<0.001*
Presence of a Median	-0.97	0.26	-3.67	-1.49	-0.45	<0.001*
Distance to Cover	-0.011	0.0079	-1.43	-0.027	0.0042	0.15
RED SQUIRRELS						
Type Wooden (DWC)[a]	0.83	2.25	0.37	-3.57	5.23	0.93
Type Pipe (PC)[a]	1.08	1.58	0.68	-2.03	4.18	0.78
Comparison PC - DWC[a]	0.24	1.88	0.13	-3.44	3.93	0.99
Openness	5.25	2.90	1.81	-0.42	10.9	0.070
Presence of a Median	-1.56	1.86	-0.84	-5.20	2.09	0.40
Distance to Cover	0.011	0.037	0.29	-0.063	0.084	0.78

[a] Output obtained from pairwise comparison.

Appendix: Life History Traits and Natural History

Species	Lifespan (in wild)	Diet	Activity patterns	Sociality	Territoriality	Home range size	Distribution	Reproduction	Reproductive maturity	Annual reproductive output	Primary predators
American Marten	4 yrs	carnivore	cathemeral	solitary	territorial	320 - 3000 ha	most of Canada	MF-MM	15-16 months	1 litter, 1-5 (3 avg) born	foxes, raptors, lynx, wolves, and fishers
American Mink	3 yrs	carnivore	nocturnal	solitary (pair in mating season)	territorial, but tolerant	150 - 1600 ha	most of North America	MF-MM	10-12 months	1 litter, 1-8 (4 avg) born	raptors, red foxes, lynx, and otters
Cinereous Shrew	5-16 months	insectivore	cathemeral	solitary	territorial	no clear range	most of Canada	considerable variation	2 months	1-3 litters, 1-12 (5-7 avg) born	raptors, snakes, weasels, foxes, fish, and other shrews
Common Muskrat	3-4 yrs	omnivore	cathemeral	solitary (pair in mating season)	territorial	no clear range	most of North America	F-M	1 yr	2 litters, 1-14 (5-9 avg) born	raptors, foxes, mink, raccoons, fishers, otters, wolves, lynx, and humans
Deer Mouse	1 yr	omnivore	crepuscular	solitary (loosely)	territorial (breeding females)	0.1 - 1.2 ha	most of North America	MF-MM	1-2 months	1-4 litters, 1-8 (3-6 avg) born	raptors, weasels, foxes, skunks, snakes, and other rodents
Eastern Chipmunk	2-5 yrs	omnivore	diurnal	solitary	territorial	0.01 - 1 ha	eastern Canada	MF-MM	delay reproduction until second season	2 litters, 1-8 (4-5 avg) born	snakes, weasels, raptors, and foxes
Ermine	1.5 yrs	carnivore	cathemeral	solitary	territorial	1 - 87 ha	circumboreal	MF-MM	1-2 months (F), 11-12 months (M)	2 litters during life, 1-18 (4-8 avg) born	raptors, foxes, snakes, humans, and other weasels
Jumping Mouse	1 yr	herbivore	nocturnal	solitary	territorial, but tolerant	0.08 - 1.10 ha	central Canada	MF-MM	1-3 months	2-3 litters, 2-9 (4-5 avg) born	raptors, foxes, weasels
Long-tailed Weasel	3 yrs	carnivore	nocturnal	solitary	territorial	16 - 240 ha	southern Canada	MF-MM	3-4 months	1 litter, 1-9 (4-5 avg) born	foxes, raptors, humans, and other weasels
Marmot	4-5 yrs	herbivore	diurnal	solitary (loosely)	territorial	no clear range	central Canada	MF-MM	2 yrs	1 litter, 1-9 (3-4 avg) born	weasels, foxes, mink, and humans
Meadow Vole	2-3 months	herbivore	diurnal	solitary (loosely)	territorial (breeding females)	0.040 - 0.35 ha	most of Canada	MF-MM	25-45 days	2-4 litters, 1-11 (4-6 avg) born	raptors, snakes, foxes, weasels, wolves, and lynx
North American Beaver	10 yrs	herbivore	nocturnal	social	territorial	0.5 - 43 ha	most of North America	F-M	1.5-3 yrs	1 litter, 1-9 (2-4 avg) born	humans, wolves, lynx, bears, mink, and otters
North American Porcupine	8-10 yrs	herbivore	diurnal	solitary (loosely)	territorial	1.5 - 59 ha	most of North America	MF-MM	18-25 months	1 litter, 1 born	fishers and foxes

Species	Lifespan (in wild)	Diet	Activity patterns	Sociality	Territoriality	Home range size	Distribution	Reproduction	Reproductive maturity	Annual reproductive output	Primary predators
North American Pygmy Shrew	1 yr	insectivore	nocturnal	solitary	territorial	unk	most of Canada	unk	unk	unk	snakes, raptors, weasels, and other shrews
North American River Otter	13 yrs	carnivore	nocturnal	social	depends on region	2000 - 4000 ha	most of North America	MF-MM	21-24 months	1 litter, 1-6 (1-3 avg) born	wolves and humans
North American Water Shrew	18 months	insectivore	crepuscular	solitary (pair in mating season)	territorial	unk	most of Canada	F-M	9 months	2-3 litters, 3-10 (5-6 avg) born	snakes, weasels, raptors, fish, and frogs
Northern Short-trailed Shrew	14-17 months	omnivore	nocturnal	solitary	not territorial	no clear range	eastern Canada	MF-MM	2-3 months	4 litters, 3-10 (4-6 avg) born	raptors, snakes, weasels, skunks, and foxes
Raccoon	2-3 yrs	omnivore	crepuscular	solitary	territorial (males only)	5 - 2560 ha	southern Canada	MF-MM	22 months	1 litter, 1-7 (3-4 avg) born	wolves, fishers, foxes, and raptors
Red-backed Vole	10-12 months	herbivore	cathemeral	solitary	territorial	0.01 - 0.50 ha	most of Canada	MF-MM	2-4 months	2-3 litters, 1-10 (4-6 avg) born	raptors and weasels
Red Fox	3-4 yrs	omnivore	nocturnal	solitary (pair in mating season)	territorial	400 - 3500 ha	most of North America	F-M	8-10 months	1 litter, 1-12 (4-8 avg) born	wolves, lynx, and humans
Red Squirrel	5 yrs	omnivore	diurnal	solitary	territorial	0.24 - 0.35 ha	most of Canada	MF-MM	1 yr	1 litter, 1-8 (2-4 avg) born	raptors, snakes, martens, fishers, foxes, lynx, weasels, and mink
Snowshoe Hare	5 yrs	herbivore	nocturnal	solitary	territorial	1.5 - 12 ha	most of Canada	MF-MM	1 yr	2-3 litters, 1-9 (2-5 avg) born	lynx, wolves, foxes, fishers, martens, mink, weasels, raptors, and red squirrels
Star-nosed Mole	unk	insectivore	cathemeral	unk	unk	unk	eastern Canada	unk	10 months	1 litter, 2-7 (5 avg) born	raptors, skunks, weasels, fish, and frogs
Stripped Skunk	4 yrs	omnivore	nocturnal	neutral	territorial, but tolerant	120 - 490 ha	most of North America	MF-MM	10 months	1 litter, 1-10 (5-7 avg) born	raptors and foxes

Information sourced from Naughton 2012.

Abbreviations include:

- yr(s): year(s)
- unk: unknown
- ha: hectare
- avg: average
- F: female
- M: male
- MF: multi-female
- MM: multi-male